I also continue to be impressed by many of the great German plant physiologists from the end of the nineteenth century and would recommend plant scientists to consult their work. Although I am unable to read the original papers, their work is available in translation through their truly magisterial textbooks: Haberlandt (*Physiological Plant Anatomy*), Pfeffer (*The Physiology of Plants*) and Sachs (*On the Physiology of Plants*). Because these scientists were superb anatomists and experimenters, these books are still treasure troves of phenomena that could be profitably re-investigated. More recently, two scientists I have always admired are Professors Enid MacRobbie and Klaus Rachke, both real titans in the field whose work is marked by great rigor and insight. Of their considerable output, I would pick two reviews as having been especially influential. Enid's review in the *Phil. Trans.* (1998) of the control of the ion fluxes that underlie stomatal movements is a landmark, and has influenced a generation of plant scientists, while Prof. Rachke's chapter in the *Encyclopedia of Plant Physiology* (Volume 7, 1979) on stomatal movement is as remarkable for its deep understanding of the system as it is for its prescience. I read these again and again.

Vacations, do you take them and if so where do you go and what do you read? Yes, I certainly do. We tend to go to the Orkney Islands or the north of Scotland. This year my wife and I went with two of our children (who are PhD students in plant sciences) and their partners to Scourie in the extreme northwest of Scotland and Ardgay on the river Carron on the East Coast. The walking was outstanding and I especially enjoyed visiting Amat Forest, which is a relic of the Caledonian Forest which dominated the Scottish landscape. As for books, among other books I re-acquainted myself with *The Pickwick Papers*. Dickens' power of characterization is of course wonderful (I also enjoy Trollope greatly), and I challenge any University academic not to smile wryly at his descriptions of the meetings of the Pickwick Club.

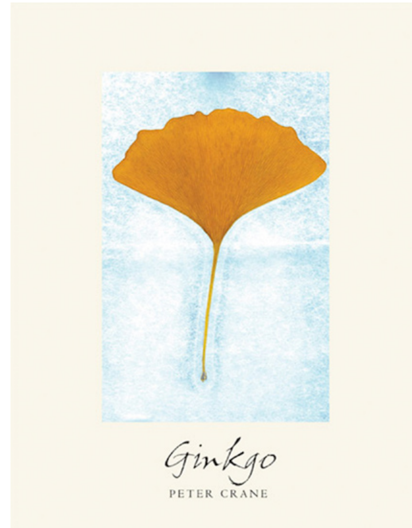
University of Bristol, Woodland Road, Bristol, BS8 1UG, UK.
E-mail: Alistair.Hetherington@Bristol.ac.uk

Book review

Ginkgo still on the go

John A. Raven

Ginkgo: The Tree that Time Forgot
Peter Crane
(Yale University Press, New Haven and London; 2013)
ISBN: 978-0-300-18751-9



Ginkgo biloba, with its characteristic fan-shaped leaves, is a commonly planted street tree in cities in the temperate zone, and has religious significance in the Far East, so it is familiar to many people. Botanically, *Ginkgo* is a gymnosperm — a seed plant with naked seeds — but is not clearly a close relative of any other extant gymnosperm. As a genus, *Ginkgo* is a true living fossil — a fossil species (*Ginkgo cordilobata*) was found in rocks of Early Jurassic age, about 190 million years ago. After the Jurassic, *Ginkgo* and its relatives diversified, and 100 million years ago (Cretaceous period), *Ginkgo* and its relatives, as well as *Ginkgo*-like foliage, occurred in many temperate habitats worldwide. Since the Cretaceous, there has been a loss of diversity and a contraction of range of the *Ginkgo* alliance — today there is just one species, *Ginkgo biloba*, native to China. The extent to which human protection has ensured the survival of *Ginkgo biloba* until the present is not clear.

My first day-to-day contact with *Ginkgo biloba* was as an undergraduate where a female and a male *Ginkgo* tree were trained up the back (south) wall of the Botany School, the home of what was then the University of Cambridge's Botany Department. As a postdoc there, I performed my only minimal experiment on *Ginkgo*, published in 1972. I developed an interest in, and an affection for, *Ginkgo*, but am hardly an expert. However, I eagerly agreed to review Peter Crane's book *Ginkgo: The Tree that Time Forgot*, despite my wondering about an entire book devoted to one tree species out of the quarter million or more species of seed plants, of which about 100,000 are trees. Peter Crane's scholarly and entertaining book triumphantly justifies this investment of cellulose, presumably from trees other than *Ginkgo*, in its seven sections and 37 chapters.

Crane assumes relatively little botanical background in his readers, and after a three-chapter prologue he discusses *Ginkgo* in the context of the physiology and growth of trees in general, emphasising the particular features of *Ginkgo*. Importantly, he neatly demolishes the idea that *Ginkgo,* whose water-conducting tissue has relatively frequent cross walls, does not make the conducting system inferior to that of most flowering plants with much less frequent cross walls. Growth is of no evolutionary use unless it results in multiplication of the number of organisms, and Crane devotes three chapters to reproduction. He details the discovery of *Ginkgo's* motile male gametes, and emphasises the occurrence of separate male and female plants, and why older male plants sometimes produce functional female structures, but not vice versa for female trees. Crane also points out that pollination and fertilization do not commonly occur after the ovules have dropped from the tree, contrary to what I recall from my undergraduate lectures 53 years ago.

The next two parts of the book deal with the origins, subsequent evolution and present state of the *Ginkgo* group. Peter Crane is, among other things, a paleobotanist and an evolutionary biologist, and he is clearly in his element here as he ranges from the enigmatic origin of the *Ginkgo* alliance at least 220, and probably 245, million years ago, through its evolutionary radiation to become an important tree in appropriate habitats in temperate regions worldwide, to its subsequent decline in diversity and geographical range resulting in the single surviving species, *Ginkgo biloba.* What caused this decline in the range and diversity of the *Ginkgo* alliance? Crane mentions the possibility that it was loss from the area inhabited by *Ginkgo* of the mammals that disperse the seeds that underlies the contraction of range of *Ginkgo* and its relatives. More generally, Crane discusses the role of chance in the extinction of species, rather than a lack of competitive ability. *Ginkgo* survived the K–T boundary event that marked the extinction of the dinosaurs, and, less widely mentioned in television documentaries, the cycadeoids, a clade of vegetatively cycad-like gymnosperms.

The next section addresses the history of the interactions between humans and *Ginkgo*; taking a suitably critical approach, Crane places the earliest reliable written mention of *Ginkgo* in China, the country in which the relict natural population occurred, at just over a thousand years ago (980 CE). This earliest historical record is probably less than the age of the oldest Chinese *Ginkgo* alive today, although there are problems with ageing the old giant trees. Crane also considers the role that humans could have had in preventing the extinction of *Ginkgo*, and the transfer of the tree to Korea and to Japan where it was no longer native. *Ginkgo* has long been planted at religious sites in eastern Asia — Crane mentions that protection of a large old *Ginkgo* tree at a shrine in Korea extends to erecting a lightning conductor beside it to limit the possibility of damage from lightning strikes.

The naming of *Ginkgo* is, as Crane points out, a complex issue, as are so many aspects of the plant, not least because it is not easy to determine the plant to which a given name in old documents refers. Regardless of the origin of its western name, *Ginkgo* is known to have been cultivated in the western world since the 18th century.

The book then turns to the non-religious uses of *Ginkgo* in gardens and as street trees, as well as the use of the nuts in human nutrition and of various parts of the plant in pharmacy. As with so many plant products, there is still debate on the efficacy of *Ginkgo* leaves in human health.

Crane ends by considering the possible future of *Ginkgo*, in the context of more general considerations of conservation. Crane considers the conifer *Wollemia nobilis*, discovered in 1994 in the Blue Mountains of NSW, Australia. The native population of only just over a 100 trees means that it is very prone to ‘bad luck’, such as the extensive bush fires of October 2013 in the Blue Mountains. Speedy action by the authorities in NSW secured the native sites, and through vegetative propagation there are now tens of thousands of *Wollemia* growing in many parts of the world. Crane also cites cases in which rare plants remain at great risk.

Work on *Ginkgo biloba* and its fossil ancestors has, of course, continued since Peter Crane’s book was published in early 2013. An example of a recent study concerns a hanging fly (Mecoptera), whose wings appear (to humans, at least) very similar to the deeply divided leaves of a ginkgoacean plant from the same strata in the Middle Jurassic.

The book is clearly and engagingly written, with several points exemplified from Peter Crane’s own experience. It has an excellent index. The text is very well referenced in the numbered footnotes which are combined at the end of text, and its half-tone illustrations are much to my taste. I thoroughly recommend this scholarly and entertaining book to anyone who is interested in not just *Ginkgo*, but more widely in plants, fossils (living and otherwise), and how humans interact with plants.

Division of Plant Sciences, University of Dundee at the James Hutton Institute, Invergowrie, Dundee DD2 5DA, UK.
E-mail: john.raven@dundee.ac.uk

Quick guide

Casparian strips

Niko Geldner

What are Casparian strips? Casparian strips are a cellular feature found in the roots of all higher plants. They are ring-like, hydrophobic cell wall impregnations. These impregnations occur in the endodermis, an inner cell layer that surrounds the central vascular strand of roots (Figure 1). Every biology student has to learn about Casparian strips in their basic botany course, but most people quickly forget about them.

Why the funny name? They were named after their discoverer, Robert Caspary, a German botanist in the 19th century. It’s very rare in the botanical literature to name something after a person — no idea why it happened in this case, maybe because the name sounded pretty cool.

What are they there for? Casparian strips have pretty much the same function as tight junctions in animal epithelia. They were shown to provide an extracellular (paracellular) diffusion barrier within the plant roots, forcing nutrients to pass into the cells and thus to be subjected to the action of plasma membrane transport proteins. Plant researchers refer to this as an ‘apoplastic’ barrier, because the interconnected cell wall space between cells is referred to collectively as the ‘apoplast’. The extracellular apoplast contrasts with the ‘symplast’, which is the interconnected space of the cytoplasm of different plant cells (connected through plasmodesmata — another cool, plant-specific feature).

Why are Casparian strips located in an inner cell layer? This is a good question — why would you put an extracellular diffusion barrier so deep within the root as opposed to blocking diffusion at the epidermis? There is no good answer to this (but then, ‘why’ questions are always a bit unfair...). I often like